A CONTRIBUTION TO THE THEORY OF ORTHOGENESIS [1].

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SEVERAL reasons have been given why biological discussion has, for a number of years, ceased to center about the fact of evolution and is now chiefly concerned with the factors, for such is evidently the case: the principal aim of modern biological researches is apparently to throw light upon the question of method. It is now a part of common knowledge that Darwin considered the natural selection of fluctuating variations to be the principal factor in evolution, and some of his successors have gone so far as to see in it a sufficient one; but, while few biologists will probably be disposed to deny that natural selection is an efficient factor in evolution, there seems to be now on hand a sufficient body of data to show that it is far from being the only one. Among other methods[2] that have been emphasized, mutation and orthogenesis may be mentioned, each of which has its adherents, and it is the last named of these that seems to be the principal one concerned in the evolution of a group of snakes that I have recently monographed—the genus *Thamnophis* (the garter-snakes).[3]

I will briefly summarize the conditions that prevail in this group:

1. The genus *Thamnophis* consists of four groups of

[1] Read at the Darwinian Celebration of the Michigan Academy of Science, April 1, 1909.

[2] I mention only these three (selection, mutation and orthogenesis), as they appear to me to be the only ones that can be considered to have been dominant methods in the evolution of the forms in the genus that constitutes the basis of this discussion.

[3] Ruthven, Alexander G., "Variations and Genetic Relationships of the Garter-snakes," Bull. 61, U. S. Nat. Museum.

closely related forms, each group ranging both northward and southward from the Mexican plateau (which is their center of dispersal) into North and Middle America.

2. Each group consists of a series of forms, the ranges of which adjoin and correspond to different geographical regions.

3. The forms of the same group may intergrade or not, but in either case they come in contact where the geographic conditions with which they are associated meet, and the areas of transition in characters correspond to the areas of intermediate environmental conditions. When the forms intergrade the transition in characters takes place gradually in the intermediate region, and where there is apparently no intergrading at present the two forms become most like each other in this region, there being no abrupt changes in characters between two directly related forms.

4. Each group tends to become progressively more dwarfed away from the Mexican plateau, each form usually being more dwarfed than its neighbor toward the center of origin, and less so than the representative whose range adjoins it on the side away from the center.

5. The relative size is correlated with the number of labials and rows of body scales, and these two characters —size and scutellation—constitute the only apparent specific differences, except in the few cases where they are accompanied by differences in color or relative tail-length.

6. The amount of dwarfing is not associated with particular geographic regions, but the scutellation and relative size of any form is that of its immediate ancestor plus the dwarfing which it has itself undergone. Thus a dwarf form of one group frequently occurs in the same region with a much less dwarfed representative of another group, the difference in relative size being due to differences in the number of forms between the one in question and the center of origin.

7. The variations in the characters of each form fluctu-

ate about a mean, and the transition in characters between the different forms is brought about by a gradual variation of the average type.

Students of evolution problems will recognize in this summary (*a*) the old story of the association of different forms with different environmental conditions, (*b*) the so-called definite or determinate evolution, and (*c*) that the phylogenetic variations are gradual.

It has long been noted that, among animals of the same group, the different forms are generally associated with different environmental conditions. In some cases it seems that these forms may occupy different habitats in the same environment, but in by far the greater number of instances, at least among terrestrial animals, directly related forms inhabit different, but neighboring, geographic areas. That there is some connection between the differentiation of such a group and the diversities of the region it occupies has usually been assumed; at least it is a fact that must be considered in any explanation of evolution. It is explained by natural selection on the assumption that the different conditions in the two regions demand different adaptations on the part of the organism, but this explanation will apparently not hold in the case of the garter-snakes, for there is certainly no advantage in dwarfing *per se*. It might be assumed (and it would be pure assumption) that this trait is correlated with unperceived adaptative characters, but this would seemingly be trying harder to save the theory of natural selection than to explain the facts. I have pointed out that there is no relation between the amount of dwarfing and particular habitats, but that forms (belonging to different groups) of quite diverse scutellation may occupy the same region. Apparently the conditions in each region do not call for a particular size (as would, it seems to me, be *approximately* the case if the struggle for existence in each habitat required that the forms become dwarfed), but only act to modify to some extent the invading form, the relative size of the latter being

determined as much by the modifications which the group has previously undergone as by those to which the particular form has been subjected.

I believe that these objections to the operation of selection in the evolution of these forms also argue against De Vries's mutation theory as an explanation, for, while it is easily conceived that mutations may have arisen within the limits of fluctuating variation in each case, we must also assume that the new form pushed into the new environment, or at least now occupies it to the exclusion of immediately related forms, because better fitted for it, which does not seem to be the case. What seems to have actually taken place is that as each group pushed out from the center of origin it became modified each time it encountered a new region of environmental conditions, not by the selection of forms better adapted to the new conditions, but by the modification of the entire section that invaded the new region. This may be tested more thoroughly by an examination of the method of evolution.

Perhaps the most striking characteristic of this genus is the manner in which evolution has taken place along definite lines. Although the forms frequently have other distinctive characters, they nearly all have this in common that they are more dwarfed than the form from which they have been derived, and there is no case in the genus where a form is larger than its neighbor toward the center of origin. The history of each group has thus been one of progressive dwarfing as it departed from the center of dispersal.

It is too often overlooked by students of evolution that natural selection can cause directed evolution (orthoselection); for in order that it may do so it is only necessary that there be an accruing advantage in the increased development of a character. The characters must thus be utilitarian, however, which is apparently not true in this case. Moreover, it would certainly be taxing the theory to make it account for the continued development

in the same direction in the four groups, when one considers the great variety of conditions with which they are associated. To explain this definite development on the basis of orthoselection it would be necessary to adopt the point of view that each form in each group found it of advantage in the struggle for existence in its particular environment to become more dwarfed than its immediate ancestor, which is to my mind unthinkable when one considers that we have in this genus four groups that push out in all directions from the center of origin, into desert, grassland and forest regions, in the tropical and temperate zones, and yet in every case the modifications associated with each region are practically of the same nature and non-adaptive. We meet the same difficulties if we attempt to apply the mutation theory to explain this definite evolution, for, while de Vries's mutants arise suddenly and are definite steps in new directions, he states in regard to the accumulation of characters:[4]

> It is not by mere chance that the variations move in the required direction. They do go, according to Darwin's view, in all directions, or at least in many. If these include the useful ones, and if this is repeated a number of times, cumulation is possible; if not, there is simply no progression, and its type remains stable through the ages.

It seems from this that in order to explain the evolution of a group by a series of modifications more or less similar in kind the mutation theory of de Vries is forced to fall back upon natural selection. If I have rightly interpreted the conditions, I believe that natural selection, with or without the assistance of the mutation theory, fails as an explanation of the definite evolution of this genus, and that we have here an example of true orthogenesis, *i. e.*, progressive modifications in each group without the aid of natural selection.

The nature of the variations is very interesting in several ways, and throws further light on the problem, for, although one must be cautious of forming conclu-

[4] De Vries, H., "Species and Varieties, Their Origin by Mutation," p. 572.

sions on this subject without the controlling evidence of experimentation, certain general relations seem to be apparent.

I have stated that the variations in each form fluctuate about a mean, but that this mean varies, approaching in the intermediate region that which characterizes the next form on its line of descent. That the different forms also originated in this way is shown in the numerous instances where they actually intergrade. This is essentially the idea of mutation (in the sense of Waagen and Scott) or "phylogenetic variation", which is not to be distinguished from individual variation by any character of quality or quantity, but by the fact that it pursues a determinate direction by the gradual shifting of the normal type. Conn[5] states that:

> It should be noticed that these considerations in regard to variations along definite lines have less significance in connection with such characters as can be supposed to advance by general averages. Some organs have been advancing in definite directions for long generations, but if the advance consists of an increase or decrease in size of the organs there is not needed any law of determinate variation to explain the matter. If it be an advantage to have an organ increase in size, and if variations in this organ occur around an average type, then without any necessity of supposing a special law directing variations, we can understand how natural selection will continue to increase the size of the organ in question.

All this is very true, for it is only orthoselection working on the average type, but as selection seems to be debarred in this case, the characters being non-utilitarian, we apparently have in the garter-snakes a case of evolution along fixed lines as the result of definite variation. Even if we could admit the selection of fluctuating variations as the dominant factor in the evolution of these forms, we should encounter the additional difficulty that it (selection) is apparently unable to create a new species, the form slipping back to the original condition when the selection ceases. The nature of the variations also seems to me to debar de Vries's theory of mutations as a

[5] Conn, H. W., "The Method of Evolution," p. 146.

possible explanation, for, according to de Vries, the specific changes are sudden and fixed, the new race appearing fully formed, which is certainly not the case in these snakes, unless we consider the new race as having been formed by small successive mutations of the same kind, which would, if I understand him rightly, be contrary to de Vries's idea of mutations, for he says that they "take place so far as experience goes without definite direction." We have apparently in these snakes an example of definite but gradual variation, in that there is in each group a gradual development of forms along a fixed path, without the aid of natural selection.

A theory that accounts for the definite evolution of this genus without the aid of selection is that there has been in each group a gradual modification of the forms under the influence of the environment. The determinate variation of the average type, the close association of the forms with different geographic regions and the consequent correspondence of areas of transition in characters with intermediate geographical conditions, would seem to render this conclusion unavoidable, if, as seems evident, selection is not operative here. It should be noted, however, that, while the evolution of the genus has been distinctly orthogenetic and associated with the environment, it does not appear that the latter has, as has often been supposed by adherents of this theory, a specific effect. This would be difficult to determine if we were dealing with one group, for example one that pushed northward from the Mexican plateau, for here there would be an increasing difference in climatic conditions, associated with accumulated modifications, between the range occupied by the form at the center and that of the most outlying species. But when all four groups are considered it is seen that the same modifications appear whether the group is pushing into the tropic or temperate regions, or into deserts, semi-arid plains, or humid forests, and it is difficult to conceive of environmental conditions common to all of the regions occupied

by these snakes that would exert such a specific effect upon them. It seems rather that throughout the genus the germ cells have such a restricted number of potential responses that the different groups have tended to vary in the same direction (homoplasy) under the influence of the environments which have been encountered; that is to say, the similarity of the response is conditioned by the constitution of the animal, the environment only acting as a stimulus upon the germ cells.

This theory would seem to satisfactorily explain why some directly related forms intergrade while others do not, for if infertility is in proportion to physiological diversity, as Darwin held, it is quite evident that as the new form produced as a group pushes into a new region becomes more or less modified, it will also probably become physiologically different from the parent stock and be more or less unable to cross back. This is essentially Eimer's Genepistasis, or Entwicklungstillstand, the standing still of certain forms at definite stages in development while others continue. But it should be noted in this case that the forms that progress each time are always associated with new geographic regions, and do not occur, as Eimer holds that they can, in the same region with the parent stock.

In conclusion I would like to point out that the purpose of this paper is to describe the method of evolution in the genus *Thamnophis* rather than to discuss the cause of the variations. It is evident that the suggested relation between the action of the environment and the nature of the response of the organism can only be tested by experimentation. I may add further that the interpretation offered of the conditions in this genus depends upon whether or not the relationships of the forms and the lines of development are as outlined. In pursuing work of this kind it soon becomes apparent that the relationships of any form can only be determined with certainty when the conditions that prevail throughout the genus have been examined carefully, and, conversely, that erroneous

ideas of relationships are very liable to result from incomplete knowledge of the course of evolution in the group, so that it is very hazardous to select a few forms of a genus and endeavor to discover the laws governing their development. An illustration can be drawn from this genus: *butleri,* which lies entirely within the range of *sirtalis,* may, so far as its characters go, easily be conceived to have been derived from the latter, and, if so, a different theory of the factors involved in its evolution must be sought to explain its origin. That it has more probably been developed from *radix* by dwarfing only becomes relatively certain when the lines of evolution in the genus have been worked out. This should discourage attempts to adduce as evidence for or against any theory the relationships of particular forms before the genus has been studied as a whole, and the general lines of development determined.